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Aliasing in peripheral vision for flickering gratings under different levels of illumination

F.A. Ennis and R.S. Anderson

Vision Science Research Group, School of Biomedical Sciences, University of Ulster at Coleraine, Coleraine, Co. Londonderry, N. Ireland, UK

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Abstract

Purpose. To assess how far retinal illumination can be reduced for sine-wave gratings phase reversing at different temporal frequencies in peripheral vision, while maintaining sampling limited resolution acuity performance, as evidenced by an aliasing zone between detection and resolution.

Methods. Computer generated sine wave gratings were presented with flicker rates from 0 to 40 Hz under retinal illumination levels of 3.5 to –0.5 log trolands. Resolution and detection thresholds were measured at 30 degrees in the horizontal temporal field using a spatial and temporal 2AFC paradigm respectively.

Results. At high illumination levels, detection acuity is higher than resolution acuity between 0 and 40 Hz indicating that resolution is sampling limited. As illumination level decreases the aliasing zone becomes narrower, especially at high temporal frequency until it disappears completely at 0.5 log trolands.

Conclusions. Peripheral resolution acuity ceases to be sampling limited below 1.5 log trolands for low temporal frequency gratings and at higher levels for high temporal frequency gratings. Sampling limited acuity was recorded for high frequency gratings under higher illumination levels which could be mediated by the M cells alone, but this is not the case for the lower levels of illumination.

Keywords: aliasing; luminance; peripheral acuity; temporal frequency

Correspondence: F.A. Ennis, Vision Science Research Group, School of Biomedical Sciences, University of Ulster at Coleraine, Coleraine, Co. Londonderry, N. Ireland, UK, Tel.: +44 (0) 1265 324883, Fax: +44 (0) 1265 324965, E-mail: fa.ennis@ulst.ac.uk

Introduction

Previous psychophysical studies have demonstrated the presence of an "aliasing zone" in peripheral vision.[1–7] The presence of an aliasing zone is accompanied by a discrepancy between detection and resolution thresholds for high contrast gratings, whereby the spatial frequency threshold for detection of gratings with the same mean luminance as the surround exceeds that for resolution. Subjectively, it is characterised by awareness of the presence of the grating (detection), but the percept is one of a stimulus of lower spatial frequency and different orientation. In other words, the aliasing zone brackets a range of spatial frequencies which are detectable but not resolvable.

The threshold spatial frequency for detection of high contrast gratings, under photopic conditions, is limited in peripheral vision by the retinal ganglion cell receptive field size (if the eyes optics are corrected), such that gratings with a half period smaller than the receptive field radius are undetectable.[5] Resolution threshold, on the other hand, is limited by the separation of the retinal ganglion cell receptive field centres, whereby gratings with a spatial frequency exceeding the Nyquist limit of the sampling array are unresolvable.[5] For central vision, where the ganglion cell field spacing corresponds to a single cone[8] the optical quality of the eye's refractive system has a cut off below the theoretical detection and resolution limits,[9–10] hence both thresholds are limited by the optics, and vision can be described as optically limited. Optical quality declines with increasing eccentricity,[11–12] as does retinal ganglion cell density.[13] However, ganglion cell density declines more rapidly than the eye's optical qualities, with a corresponding increase in receptive field size.[6,13–15] Hence resolution acuity under photopic conditions is no longer limited by the optical system, but by the ganglion cell spacing. Any discrepancy between detection and resolution thresholds therefore implies that the retinal image is under-sampled by the retinal ganglion cell layer and cannot be represented veridically. Hence resolu-

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tion acuity under these conditions can be described as "sampling limited", and as a consequence, the resolution acuity gives a direct estimate of the density of responding ganglion cell population.[16–18] The presence of aliasing is one clear sign that a task is sampling limited and an aliasing zone has been shown to be present for static gratings and for gratings which phase reverse at temporal frequencies of up to 40 Hz under photopic conditions.[4] Under scotopic conditions, resolution acuity was found to be limited by factors other than the sampling array density[19] unless the optics of the eye are bypassed, in which case an aliasing zone can again be demonstrated.[20] An aliasing zone, however, is only present if the sampling array density remains the limiting factor for resolution acuity and hence will be lost if visual function becomes limited by another factor e.g. optics or receptive field size/overlap. As contrast decreases or receptive field size increases, detection threshold increases until it becomes equal to resolution threshold, after which further deterioration results in both thresholds reducing identically.[4,21–22] However, no studies exist examining the combined effect of retinal illumination and flicker frequency upon the existence of the aliasing zone.

The purpose of this study, therefore, is to expand on previous studies to ascertain at what retinal illumination/temporal frequency combinations peripheral resolution acuity ceases to be sampling limited. Also, since magnocellular ganglion cells display greater sensitivity to flicker and respond better than parvocellular cells at low illumination levels,[23–25] we wanted to establish if aliasing can be demonstrated in a laboratory situation for experimental conditions which would be M cell dominated. This would permit better measurement of M ganglion cell density changes in ocular diseases which may selectively affect this class of cell.

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Materials and methods

For two experienced observers (the authors), we measured detection and resolution performance for high-contrast computer-generated sinusoidal gratings at 30 degrees eccentricity in the nasal horizontal retina of the right eye. The stimuli were generated using a Visual Stimulus Generator VSG2/3 (Cambridge Research Systems) and displayed on a 17 inch high-resolution computer monitor (Eizo).

The target used was a three degree radius circular patch of high contrast (90%) sine-wave grating against a background with the same mean luminance (75 cd/m^2). Luminance differences between stimulus and surround were checked for using a positive blur lens. Viewing distance was 1.5 m and off-screen fixation was maintained by a red LED. Grating orientations of 45 and 135 degrees were chosen to minimise the effect of horizontal/vertical dissimilarities in thresholds at this position in the visual field. Total stimulus duration time was 1.0 s, with 0.3 s ramping at the start and end of the stimulus presentation.

Sphero-cylindrical refractive correction for this eccentricity and distance was ascertained by retinoscopy for both subjects and worn for all measurements. A mydriatic was instilled to ensure stability of pupil size (8–9 mm for both subjects, under high luminance conditions), hence precluding a potential confounding factor due to increased peripheral aberrations when illumination levels were reduced.

Retinal illumination was controlled by a series of neutral density filters mounted in an otherwise blacked out goggle, allowing retinal illuminances of –0.5, 0.5 ,1.5 ,2.0 , 2.5, 3.0, and 3.5 log trolands. The goggle was fitted with an air-circulation mechanism to safeguard against misting of the filter. The goggles' left eye was occluded throughout the procedure. The subject was dark adapted, with the darkest filter in place, for at least 30 minutes before recording commenced. Detection and resolution thresholds were recorded at this illumination level, after which filter density was reduced in a stepwise fashion, from maximum to minimum density, allowing for smoother adaptation to the altered illumination level. For each retinal illumination level, detection and resolution thresholds were determined for a range of temporal frequencies (0, 5, 10, 15, 20, 30, 40 Hz).

Detection thresholds were measured using a 2-alternative forced choice paradigm (2AFC Temporal), where the stimulus was randomly presented at either orientation in one of two time intervals. The subject indicated within which interval they saw the stimulus by pressing one of two buttons. Resolution thresholds were measured using a 2-alternative forced choice paradigm (2AFC Spatial), whereby the subject responded as to the orientation (45 or 135) of the stimulus target by pressing one of the buttons. For both resolution and detection threshold measurements, a 3-up/1-down reversal paradigm was employed, with three consecutive correct responses resulting in a 10% increase and one incorrect response resulting in a 10% decrease in spatial frequency. No feedback was given to the subject with respect to the correctness of the responses. For both detection and resolution thresholds, seven reversals were recorded and threshold calculated as the average of the reversal values. This required 60 to 70 presentations on average for each measurement. The order in which the two thresholds, detection and resolution, were tested was also alternated from stimulus to stimulus.

Results

The graphs in Figure 1 show how detection and resolution thresholds (cycles per degree) vary with temporal frequency for the different retinal illumination levels for subjects RSA and FAE respectively. For each plot, the absence of a value indicates that the subject could not perform the task within the physical limitations of the experiment.

From Figure 1, we can see that under high illumination conditions, detection performance was significantly higher than resolution performance all the way up to 40 Hz, giving a broad aliasing zone (more so for subject RSA than FAE). For the higher retinal illumination levels we can see that both detection and resolution acuity are largely unaffected by increases in temporal frequency until the temporal frequency

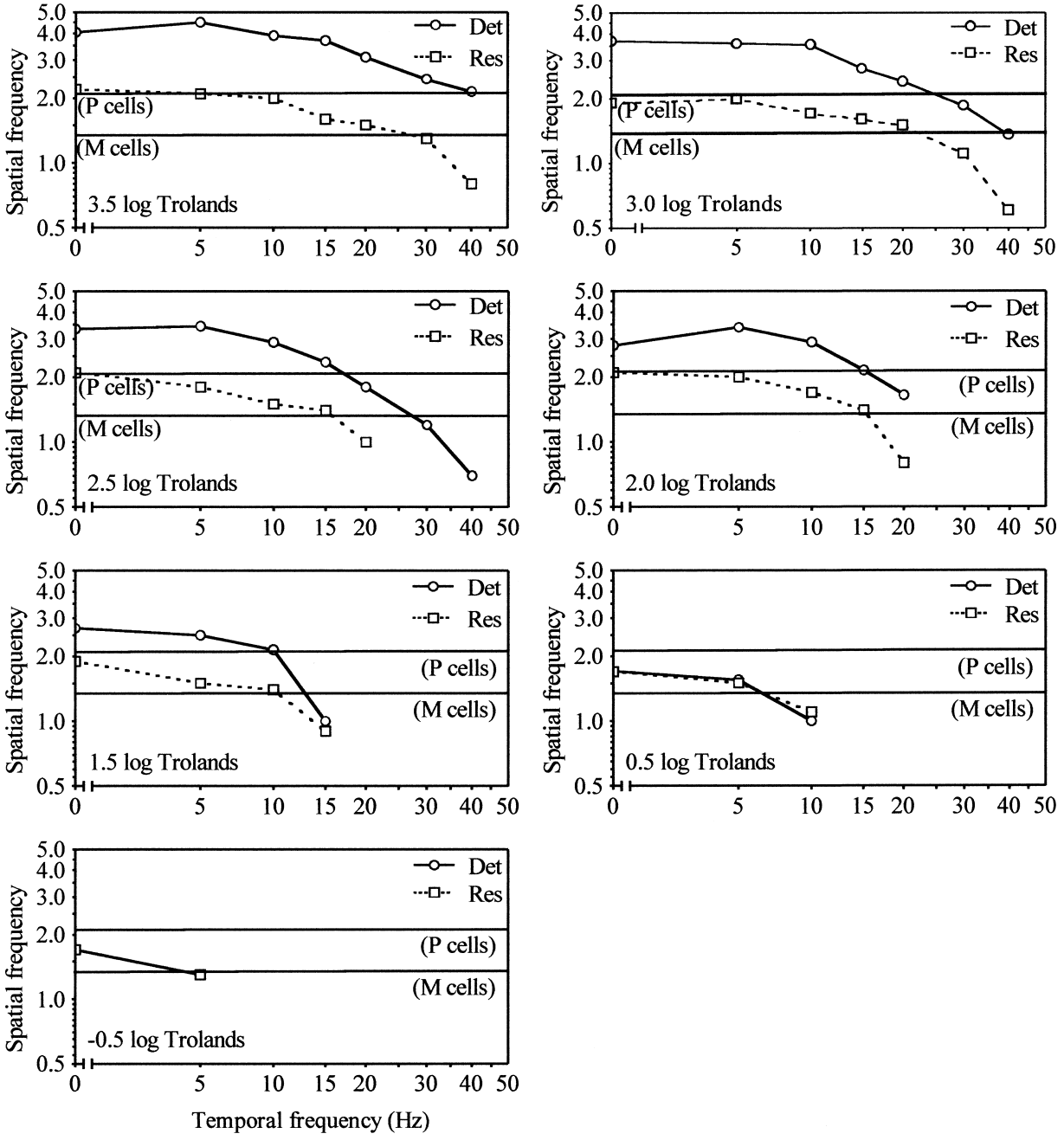

Figure 1. Threshold spatial frequency (cycles per degree) for detection (Det) and resolution (Res) versus temporal frequency (Hz) for different retinal illumination levels. The horizontal lines marked (P cells) and (M cells) denote the theoretical Nyquist limit for the P and M cell population respectively, based on the anatomical data of Dacey.[32] (Subjects RSA and FAE respectively.)

increases beyond 10 Hz, after which both decline. As retinal illumination is reduced, the aliasing zone becomes narrower, until at 0.5 log trolands detection and resolution performance are equal, with total loss of the aliasing zone for all frequencies for which it was possible to achieve a threshold measurement. While the retinal illumination levels are decreasing, the decline in performance with increasing temporal frequency occurs at an earlier stage, especially for detection acuity, resulting in convergence of thresholds with an accompanying loss of the aliasing zone at the higher temporal frequencies.

In Figure 2, the data have been re-plotted to illustrate how detection and resolution vary with retinal illumination. As the results from both subjects were qualitatively similar, we averaged the two sets of data for these plots. Each graph plots the data for the range of retinal illuminations at a single temporal frequency. We can see that for low temporal frequencies (0–10 Hz), the resolution acuity is little affected

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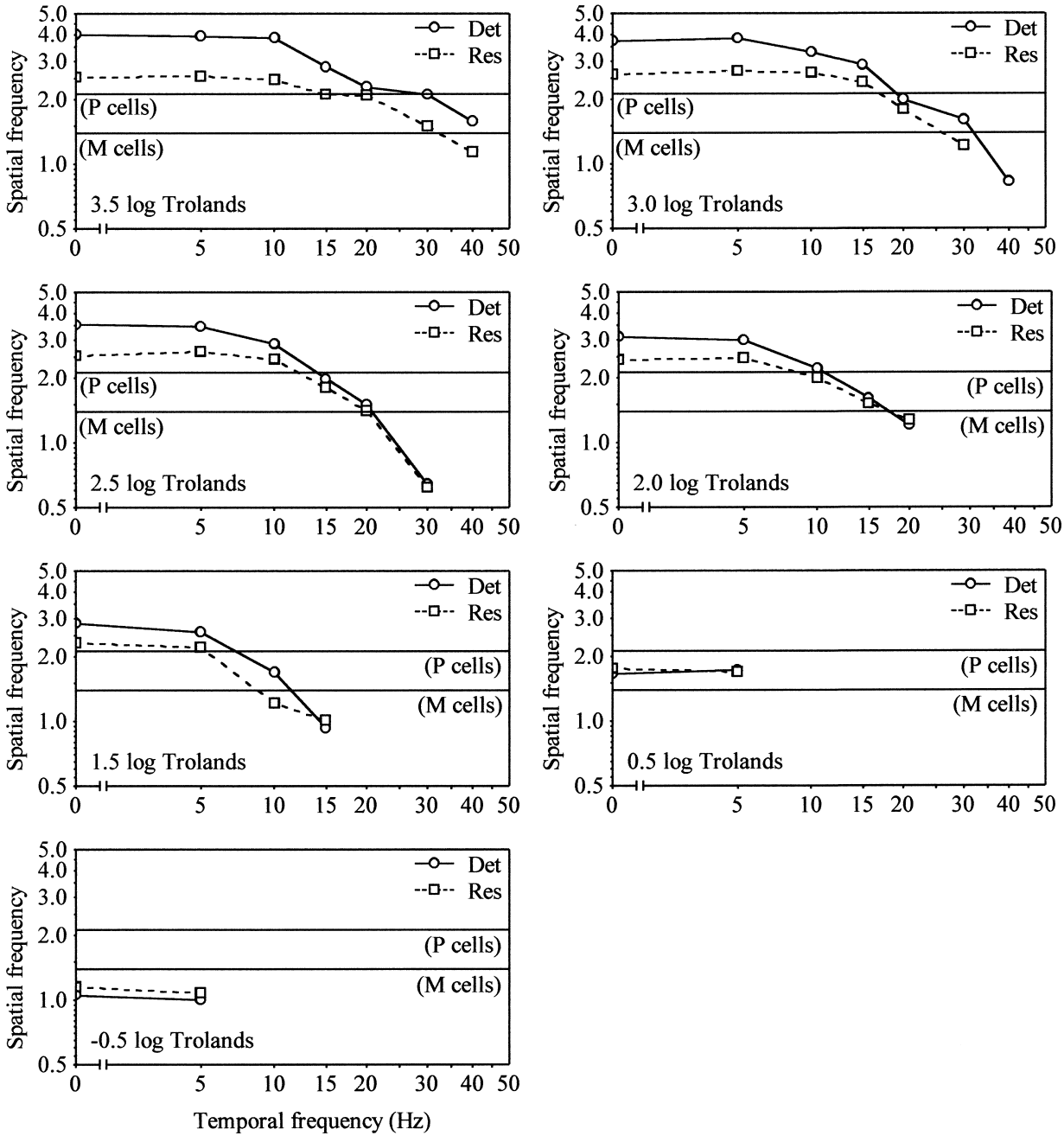

Figure 1. Continued. For legend see previous page.

by retinal illumination levels down to 0.5 log trolands, whereas the detection acuity decreases immediately and steadily with decreasing retinal illumination until, at 0.5 log trolands, detection and resolution converge, with a loss of the aliasing zone. We can also see that resolution acuity remains relatively flat until detection falls to the same level and then both decline in identical fashion. As temporal frequency increases, we find that detection and resolution thresholds remain largely unaffected at higher illumination levels, but that convergence of the thresholds occurs sooner as retinal illumination decreases.

Discussion

From Figure 1, it can be seen that for computer generated gratings of different temporal frequencies, peripheral visual acuity is sampling limited under photopic conditions all the way up to 40 Hz, in agreement with previous studies.[4,26] There is little change in either detection or resolution acuity for temporal frequencies up to 10 Hz, but as temporal frequency increases beyond 10 Hz, both detection and resolution start to decline, although the aliasing zone remains fairly uniform in width at these higher retinal illumination levels. However,

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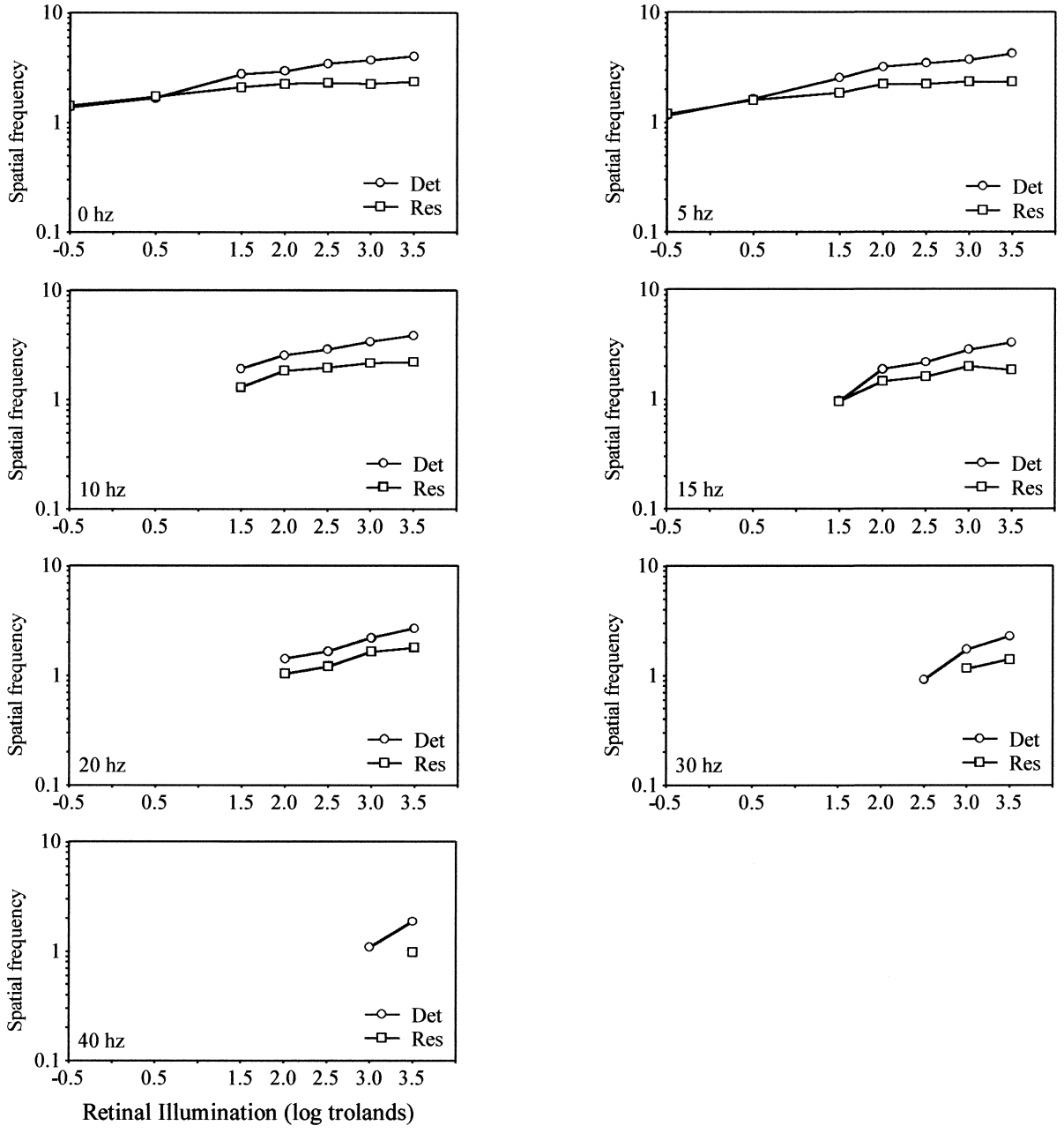

Figure 2. Threshold spatial frequency (cycles per degree) for detection (Det) and resolution (Res) versus retinal illumination (log trolands) for stimuli of varying temporal frequency. (Mean of both subjects)

as the retinal illumination decreases, we find a greater reduction for detection acuity than for resolution acuity, with a subsequent reduction in the width of the aliasing zone, especially at high temporal frequencies. Eventually, the aliasing zone is lost at around 0.5 log trolands for low temporal frequencies, and at increasingly higher retinal illumination levels as temporal frequency increases (Fig. 2). It can also be seen from Figure 2 that resolution acuity is relatively flat while there is an aliasing zone present (i.e. while resolution is sampling limited), but that detection acuity declines as soon as there is a reduction in retinal illumination levels, until eventually the two converge, after which both decline identically. The convergence of detection and resolution can be attributed, in part, to the temporal low-pass characteristics of the responding ganglion cells. Increases in temporal frequency result in a reduction in perceived contrast, hence making detection of the stimulus more difficult, requiring a decrease in spatial frequency to make the stimulus detectable again. The reduction in detection acuity becomes more pronounced with further increases in temporal frequency until detection no longer exceeds resolution. At this point, resolution is no longer sampling-limited, but becomes contrast/filtering limited. This means that resolution acuity for low temporal frequency phase-reversing gratings can only be

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considered sampling limited down to retinal illumination levels of between 0.5 and 1.5 log trolands, and at higher illumination levels for high temporal frequency phase-reversing gratings.

The reduction in sampling-limited resolution with increasing temporal frequency (Fig. 1) and/or decreasing illumination (Fig. 2) indicates that fewer retinal ganglion cells are responding to the stimulus. Parvocellular retinal ganglion cells dominate in sampling the stimulus under high illumination and low temporal frequency conditions[27] but these cells respond in smaller numbers as flicker rate increases and retinal illumination decreases, with a shift in response from the parvocellular cells to the magnocellular cell population, which are more sensitive to low luminance[28] and high temporal frequency[29] conditions. Note that there is no discreet break in the curves in Figure 1, as would be expected if there was a sudden shift in response from one cell population to the other, due to the difference in numbers of P-cells (80%) and M-cells (10%) in the normal retinal ganglion cell population.[30] Rather, there is a gradual reduction in the number of cells responding, reflecting a gradual transition from P-cell dominated conditions to M-cell dominated conditions. As with previous studies[26,29,31] this implies that there is significant overlap in the range of conditions over which P-cells and M-cells respond, and we cannot assume that one population has been totally silenced, with a subsequent monopoly of the other, for any of the stimulus conditions investigated in this study. However, the aliasing zone is lost before we reach scotopic levels, particularly for stimuli of high temporal frequency. The horizontal lines on each graph in Figure 1 represent the theoretical P-cell and M-cell resolution limits, calculated (to a first approximation) from Dacey's anatomical data,[32] assuming a regular square array. From the P-cell lines in Figure 1, it can be seen that under photopic, low temporal frequency conditions, resolution acuity is close to what is expected from anatomical predictions for subject RSA. The results for subject FAE were qualitatively similar, but the resolution acuity measurements for subject FAE slightly exceed those for subject RSA. This probably indicates a higher sampling density for subject FAE, which is entirely possible since the anatomical data has shown significant inter-subject variability in retinal ganglion cell density.[13] Looking at the predicted resolution limit for M cells it can be seen that resolution acuity under the higher retinal illumination levels utilised here, is too good at low temporal frequencies to be mediated by the M-cell population alone, but that the same stimuli conditions with higher temporal frequency display sampling limited performance at threshold levels that could theoretically be mediated by the M cell population alone. This, however, is not the case with the lower illumination levels, as reduction of retinal illumination results in resolution acuity being limited by other factors than the underlying sampling density.

This study also has clinical relevance. It has been reported that there may be a selective loss of the magnocellular population in the early stages of glaucoma,[33–34] hence measuring the resolution of the M-cell population by judicious choice of stimulus parameters and testing conditions could result in a better understanding of the disease process. Although resolution is not sampling-limited under low luminance conditions, even the use of moderate rates of flicker (e.g. 20 Hz) under reduced retinal illumination conditions (e.g. 1.5 log trolands) may permit better isolation of M cell function, and so permit better estimation of M cell density changes in ocular disease.

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